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Asymmetry compensation in a small vampire bat population in a cave: a case study in Brazil

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Abstract

Normally, the wings are assumed to be symmetrical, since radical departure from symmetry is known to hinder flight. The objective of the present paper was to investigate the symmetry of the wing structure in a population of common vampire bats, *Desmodus rotundus*. The bones of both wings were measured, and the area of each wing was calculated. Asymmetry was found, with males having a larger number of asymmetric bone structures than females. Moreover, both directional asymmetry and antisymmetry were identified for the males, whereas for the females only fluctuating asymmetry was found. However, although asymmetry does occur, it is generally compensated for by complementary changes in the structures of the other wing. We believe that by keeping the wing area symmetrical, potential aerodynamic problems may be minimized.

Keywords

Asymmetry, caves, compensation, natural selection

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Introduction

In natural populations, morphological variations in bilateral structures are frequently detected (Gannon et al. 1992), and have been studied for different groups of organisms including arthropods (e.g. Elek et al. 2014; Padro et al. 2014; Olivero et al. 2015) vertebrates (e.g. McEntee 2014; Lazic et al. 2015) and plants (e.g. Chudzinska et al. 2014; Klisaric et al. 2014). This variation is assumed to be a reflection of the evolutionary factors that have shaped organism phenotypes (Gannon et al. 1992). Different phenotypic variations are frequently distinguishable in groups, and their detection can promote the comprehension of the processes of speciation and of the maintenance of phenotypic integrity (Mayr 1964). More recently, renewed interest in this phenomenon has occurred because environmental stress can result in increased phenotypic variance (Elek et al. 2014; Lazic et al. 2015).

Three kinds of bilateral differences in morphology, known as asymmetry, are recognized: directional asymmetry, antisymmetry, and fluctuating asymmetry (Palmer 1994, Kark 2001, Palmer and Strobeck 2003). Each form of asymmetry is determined by subtracting the "size" of the left side feature from that of the right. Directional asymmetry occurs when the averages for these features in the population are statistically equivalent for the two sides of the body, although for a given, normally developed individual, the structures located on one side are larger or longer than those found on the other. Antisymmetry occurs when most individuals in a population are asymmetric, but it is unpredictable, which side of an organism shows greater development (Kark 2001, Palmer 1994). Fluctuating asymmetry occurs when a character on one side of the body is consistently larger than its partner (Fuller and Houle 2002). Both directional asymmetry and antisymmetry have great adaptive potential (Soulé 1967). Fluctuating asymmetry, on the other hand, is random variation; although it does not have yet well-understood genetic (or environmental) basis, its heritability is close to zero (Fuller and Houle 2002, Leamy and Klingenberg 2005). Thus, it seems to have no obvious adaptive value; it is characterized by an average difference between the pairs of structures close to zero and a normal distribution (Leamy et al. 2001, Juste et al. 2001).

Bats make up one of the most diversified groups of mammals in the world (Simmons 2005). The most highly adapted aspects of bats are their wings. Although bats are under several stressors related to land use changes, possible asymmetry in these structures has not been systematically investigated, nor has the possible effect of such asymmetry on the wings function.

The common vampire bat (*Desmodus rotundus*) has a special appeal to researchers due to its unique diet of blood and its consequent role in the transmission of serious illnesses, such as rabies. Moreover, it has a widespread distribution throughout the Neotropical region and as such, it is one of the most widely studied bat species in the world (Greenhall and Schmidt 1988). Deforestation for logging and agriculture has reduced the number and abundance of prey species and brought the vampire bats into contact with livestock, leading to several methods of population control (Johnson et al. 2014). Furthermore, this species is also unique in some aspects of its biology (e.g.

its reliance on quadrupedal locomotion, flying with a heavy blood-meal, etc) what makes it an interesting model to study asymmetry, since natural selection should act to minimize fluctuating asymmetry in traits that are most functionally important to an organism (Gummer and Brigham 1995).

Few studies have investigated the asymmetry of wing structures, despite the special ecological and evolutionary importance due to their role in chiroptera flight (Gummer and Brigham 1995, Voigt et al. 2005, 2008). Accordingly, considering the stress susceptibility of the species, we were interested in determining whether there is indeed one of the three kinds of asymmetry between wing parts and wing areas in a population of *Desmodus rotundus*, or whether localized asymmetry has been compensated for by opposite changes in the adjacent structures. We hypothesized that asymmetry of individual structures of the wing will be larger than wings' area asymmetry, due to their significance for flying.

Materials and methods

The colony of *D. rotundus* chosen for this study roosted in a quartzite cave (Gruta do Lobo cave – 21°32.581'S, 44°48.496'W) located in the municipality of Luminárias in the southern part of the state of Minas Gerais, Brazil. The natural vegetation is that of the Cerrado (Brazilian savannah), which was originally characterized by woody shrubs and grass, although recent anthropic activity, especially agriculture, has led to extensive modification. The economy of the region is based largely on farming and cattle raising, as well as the extraction of quartzite.

Eight netting sessions were made during the period from August 2006 to March 2007. Mist nets were installed at the main entrances (one per entrance) of the caves in the late afternoon (6 pm) and removed some six hours later. The individuals captured were put into cotton sacks until they could be measured in the field, individually identified with numbered collars of plastic beads and immediately released. Both males and females of a variety of ages were captured, but only adults with completely ossified articulations were actually measured for the study, since disproportional growth might be found in younger individuals. For measuring the forearm, it was protruded at an angle of 30° from the corpus and the digits at the same angle from the forearm. The caliper (precision of 0,1 mm) was oriented at an angle of 90° to the forearm (Voigt et al. 2005).

Asymmetry was determined by measuring two parameters: the length of the individual bones comprising the wing, and the total wing area formed by these structures. The bones measured were the forearm (tibia and fibula) and the metacarpal and first phalanges of the third digit, metacarpal and first and second phalanges of the fourth and fifth digits. These measurements were taken for both of the wings, comprising a total of 18 measurements for each individual. Because of their strength and ability to deliver serious bites, bats were immobilized by two persons while another person made and recorded the measurements. All morphometric measurements were taken from rigid wing structures (bones), which can be more precisely measured in the field.

On the other hand, wing´s membranes are elastic, and in order to obtain an accurate estimate, many measurements would be necessary in the field. Such sequential measurements would certainly increase the stress (and suffering) of the animal, also increasing the risk of manipulating the specimens in the field by the researchers. It is important to mention that *Desmodus rotundus* in one of the main transmitter of rabies (Johnson et al. 2014) Accordingly, we decided not to proceed the wings area measurements in the field in order to reduce the stress of the animals and also prevent potential accidents, especially because we did not know if the manipulated specimens were eventually contaminated. Hence, the wing´s area was indirectly estimated through the measurements of each wing structure presented in each wing, according to the herein proposed formula:

$$\mathbf{A = AT(M_5+P_1D_5+P_2D_5)+\{(M_3+P_1D_3)[tg30°(M_4+P_1D_4+P_2D_4)]/2\}+\{(M_4+P_1D_4+P_2D_4)[tg60°(M_5+P_1D_5+P_2D_5)]/2\}},$$

where: A = estimated area of wing (mm^2), AT = length of forearm; Mx = length of metacarpal of digit x (mm), PyDx = length of phalanx Y of digit X (mm).

The formula is based on the geometric shapes formed by the membranous parts of the wings, with the dactylopatagium and propatagium being considered to be triangles, and the plagiopatagium considered to be a rectangle (see Figure 1). The geometric forms measured were those obtained when the wing membranes are maximally distended. It is important to highlight that this formula would also allow other researchers to estimate wing´s areas based on those morphometric measures conventionally taken from bats, in those cases in which the wing´s area was not directly measured in the field. Finally, since the errors in such estimates could not be determined, we are assuming that, given the random nature of these errors, they would be equally distributed among our samples.

For each of the measurements made, including the estimate of the wing area, the differences between the right and left sides were calculated by subtracting the left side measurements from those of the right side, with negative numbers reflecting a larger left side and positive numbers indicating a larger right side. To guarantee that the magnitude of asymmetry could be compared for the different variables, the difference between the two sides was divided by the average of the two measures (right and left), thus obtaining an estimate of the relative asymmetry of each variable for that individual, as well as the percentage of difference between the two sides.

Directional asymmetry was assessed for males and females separately, by comparing the sample mean of each character to zero using a t-test (Gannon et al. 1992). Corrections for directional asymmetry were achieved by subtracting the mean asymmetry value of a character from the value of each individual for that character. Skewness and kurtosis reflect antisymmetry and were tested on correct values (adjusted for directional asymmetry) with the Shapiro-Wilk statistic for males and females separately (Gannon et al. 1992). Differences in fluctuating asymmetry between males and females were evaluated using Levene´s test. (Gannon et al. 1992).

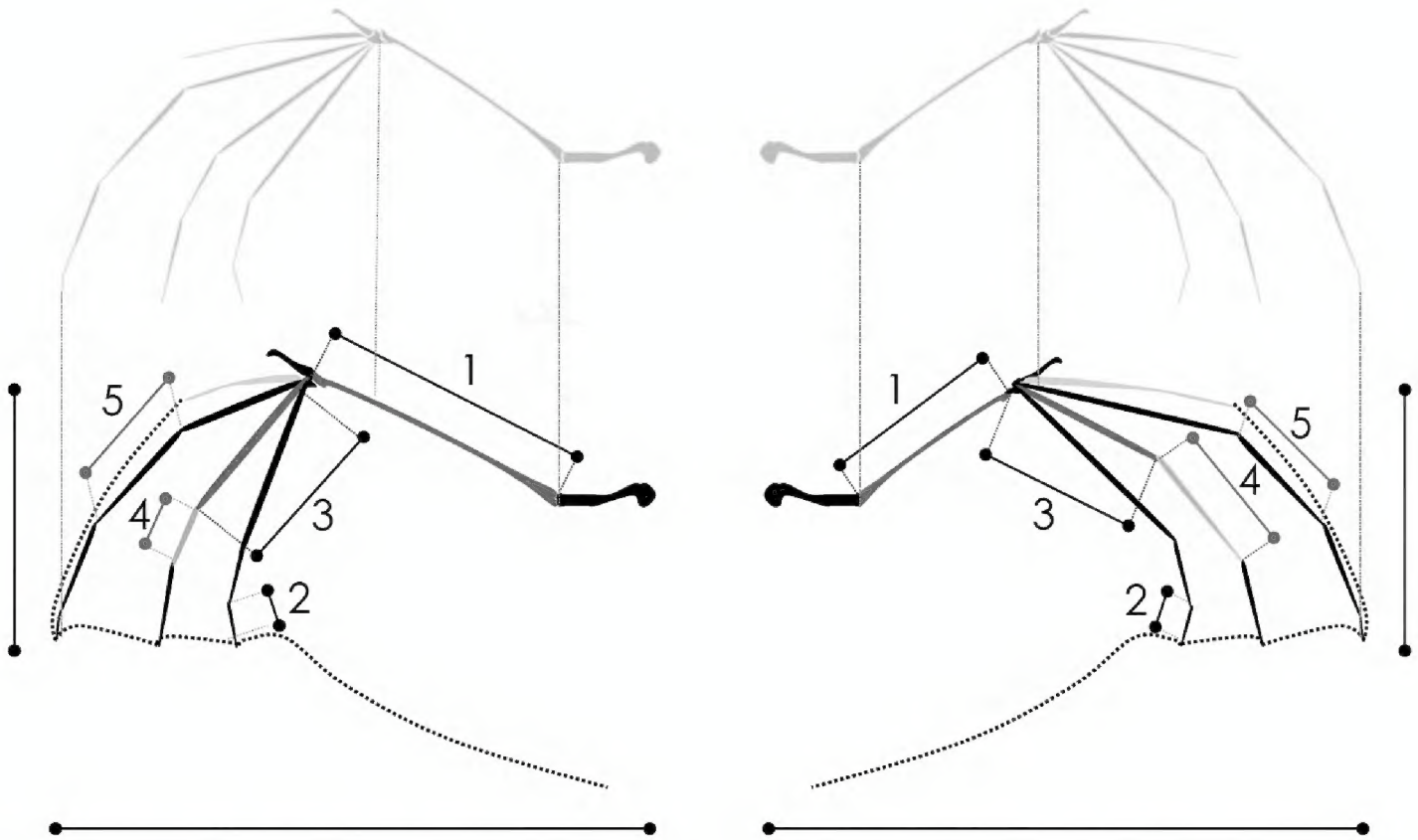

Figure 1. Graphical representation of the compensation of asymmetry in the constituent structures of the wing and the maintenance of wing area. The height of the wing remains in the various plans through inverse variation in the size of structures **3** with **4** and **4** with **2**. At length the maintenance is done by varying inversely in size from **1** to **5**. **1** forearm **2** second phalanx of the fifth digit **3** fourth metacarpal of the digit **4** first phalanx of fourth digit, and **5** first phalanx of third digit.

Compensations for asymmetry, i.e. the tendency for a given structure to increase (or decrease) on one side to balance for decrease (or increase) on the other, was verified by using a correlation matrix. For this, all the values referring to the differences observed between the structures forming the different wing areas were correlated, which made it possible to evaluate the occurrence of compensatory asymmetry.

Results

Thirty individuals of *D. rotundus* (9 females and 21 males) were captured and measured. Of the nine pairs of measures made for each individual, eight revealed significant differences between the two sides. Additionally, the wing area exhibited asymmetry. Two types of asymmetry were prevalent in males: directional asymmetry and antisymmetry (Table 1). Directional asymmetry was limited to a single structure: the metacarpal of the fourth digit (M4). Antisymmetry, on the other hand, was found for the forearm (AT), the first phalanx of the third digit (F1D3), and the area of the wing. Only females revealed fluctuating asymmetry involving the following structures: metacarpal and first phalanx of the third digit, first phalanx of the fourth digit, and metacarpal and second phalanx of the fifth digit (Table 1).

Table 1. Results for the statistical tests for asymmetry in the wing of *Desmodus rotundus*. We show the magnitude, direction and significance for different types of asymmetry. Positive values represent increased right sides. Values in bold represent values statistically significant ($p \leq 0.05$). The drift shows that the values of the structures varied more among females than among males. The $F_{(1;28)}$ statistic evaluates the equality of fluctuating asymmetry in males and females by Levene's test.

	Antisymmetry		Directional		Fluctuating	
Structure	Male	Female	Male	Female	F	Drift
AT	**0,59066**	0,90889	-0,0155	-0,2836	0,0002	-
M3	0,95412	0,86494	0,27683	-0,901	**6,3696**	F
F1D3	**0,77764**	0,86903	0,06111	0,96689	**5,6097**	F
M4	0,96294	0,96683	**0,65149**	0,8242	3,2382	-
F1D4	0,94019	0,94233	-0,8788	-3,6311	**5,6589**	F
F2D4	0,96612	0,87769	-0,1776	-1,2946	0,1464	-
M5	0,95553	0,93117	0,1186	-0,763	**14,37**	F
F1D5	0,93402	0,89801	-1,511	-2,8417	2,0735	-
F2D5	0,9272	0,93177	0,12999	3,1395	**7,1622**	F
WING	**0,315**	0,90684	0,04524	-0,0241	0,3681	-

The structures revealing the most asymmetry for males were the forearm (-1.8 to 7.6 mm) and the first phalanges of the third and fifth digits (-2 to 1.4 mm and -2 to 1.5 mm, respectively). For the females, forearm length did not reveal any significant asymmetry, although the first and second phalanges of the third digit (-5.5 to 3 mm and -4 to 5 mm, respectively) and the first phalanx of the fifth digit (-4 to 3 mm) varied greatly from one side to the other. Of the nine structures measured, only one revealed greater variation in the males (AT). Three structures (P3D4, P2D5, and P3D5) revealed similar asymmetry for the both sexes, but for the other five structures, greater variation for females was found.

Compensation was greater in females than in males. They presented less overall asymmetry in wing area found, although variation in individual structures of the wings was even greater than that registered for males. Compensation involves structures on the opposite side of the body. Thus, an increase in the fourth metacarpal (M4) on one side was accompanied by a concomitant decrease in the second phalanx of the fourth and fifth digits on the opposite side. Although female forearm length did not reveal asymmetry, the fourth and fifth metacarpals varied tremendously, as well as the first phalanges of these digits. Asymmetry of the fourth metacarpal was compensated for by concomitant increases or decreases in the length of the first phalanx of the third digit on the opposite wing, whereas differences in length of the fifth metacarpals were compensated for by variation in the length of the first phalanx of that digit on the other side. Differences in forearm length were compensated for by an increase or reduction in the length of the first phalanx of the third digit of the opposite wing (Table 2).

Not all variance of structures were compensated. In some cases, different structures change in the same way in the same side. An example of this was found to occur with the asymmetry of the fourth metacarpal, which is accompanied by the same changes in the second phalanges of the fourth and fifth digits on the same side. Likewise, this phenomenon was also observed with the fifth metacarpal and first phalange of the fifth digit.

Table 2. Table of correlation (N=29) between pairs of structures in the wings. Bold values are significant ($p \leq 0.05$). The direction is represented by the sign in front of the value. Positive sign means an increase or decrease in the size of the structure in the same direction in opposite planes. Minus sign means the opposite.

Structure	AT	M3	F1D3	M4	F1D4	F2D4	M5	F1D5	F2D5
AT	1	-0,29	**-0,38**	-0,14	0,14	0,09	-0,06	-0,33	0,02
M3	-0,29	1	0,33	0,33	-0,15	0,08	0,13	0,24	0,2
F1D3	**-0,38**	0,33	1	0,05	0,34	0,04	-0,16	-0,07	-0,21
M4	-0,14	0,33	0,05	1	**-0,38**	**0,61**	0,17	0,02	**0,56**
F1D4	0,14	-0,15	0,34	**-0,38**	1	-0,18	0,04	0,18	**-0,62**
F2D4	0,09	0,08	0,04	**0,61**	-0,18	1	0,14	-0,21	0,28
M5	-0,06	0,13	-0,16	0,17	0,04	0,14	1	**0,55**	0,18
F1D5	-0,33	0,24	-0,07	0,02	0,18	-0,21	**0,55**	1	-0,04
F2D5	0,02	0,2	-0,21	**0,56**	**-0,62**	0,28	0,18	-0,04	1

Discussion

Symmetry is the "ideal" phenotypic expression for many organisms since this maintains the body in a state of equilibrium (Gummer and Brigham 1995). Studies of the functional costs of asymmetry suggest that this condition leads to a decrease in performance during locomotion (Møller and Swaddle 1997). Moreover, it influences other activities that require the expenditure of energy, such as growth, reproduction, and immunological defense (Møller and Swaddle 1997).

Unfortunately, there are no studies regarding asymmetry in *Desmodus rotundus*. Hence, any comparisons were made with other bat species for which asymmetry studies were conducted. Gannon et al. (1992) found some asymmetry in the skull measurements of *Stenoderma rufum*, with all three types of asymmetry occurring in the same structures for the both sexes. This asymmetry was considered to reflect the genetic consequences of geographic isolation, since the population studied was endemic to the Tabonuco Forest in Puerto Rico. The effects of isolation were apparently intensified by a reduction in the population size after natural catastrophes, such as hurricanes, which are quite common in the region (Gannon et al. 1992). Asymmetry in the wing structures of *D. rotundus*, however, has been shown to follow a different pattern from that observed for *Stenoderma rufum*, with the kind and extent of asymmetry, and structures in which it occurs, varying between males and females. It is probable that the colony of *D. rotundus* studied is not isolated from other populations, nor has it been reduced by specific natural disasters. However, population reduction due to human activities cannot be excluded for the studied population, since the external area is characterized by intense mining activities.

The relation between fluctuating asymmetry and sexual selection is still a controversial hypothesis (Balmford et al. 1993, Tornhill and Møller 1998, Simmons et al. 1999, Bjorksten et al. 2000, Polak et al. 2004, Voigt et al. 2005). Thornhill and Møller (1998) found a statistically significant negative relation between asymmetry and the

success in mating in different species, with the number of individual encounters predicted to increase with a decrease in fluctuating asymmetry. Despite the fact that this is not the focus of the present study, such a fact could explain the lack of fluctuating asymmetry in males of *D. rotundus*, given that this type of asymmetry could be a limiting factor in mating success (Voigt et al. 2005, 2008). Accordingly, sexual selection could be acting under the observed asymmetry patterns, considering the *Desmodus*'s highly social behavior, although this is speculative.

Morphological asymmetry can be influenced by environmental stress, developmental instability, and genetic anomalies experienced during development (Swaddle and Cuthill 1997, Galeotti et al. 2005, Muñoz-Romo et al. 2011). Nevertheless, the occurrence of fluctuating asymmetry among female *D. rotundus* fourth and fifth metacarpals may be related to stress. Fluctuating asymmetry and other such measures of instability are usually considered to reflect incapacity to deal with genetic and environmental disturbances. Females tend to share their blood meals with other females and pups, and if blood becomes scarce, the females of a given population could undergo stress (Carter and Wilkinson 2013). This fact that might be corroborated by the appearance of fluctuating asymmetry, although other stress sources (such as mining activities) can also be acting over the studied population. Some studies show that morphological asymmetry can directly influence the ability to fly in birds. Moreover, it interferes with individual performance (Thomas 1993, Pennycuick 1989, Norberg 1990), since theoretical studies of the differential effects of wings and tails of birds suggest that asymmetry is especially costly in terms of maneuverability and flight agility (Pennycuick 1989, Norberg 1990, Balmford et al. 1993, Thomas 1993). The same may be true for the flight of bats.

Despite the existence of asymmetry in almost all structures making up the wing, in both male and female *D. rotundus*, few differences in relation to estimated wing area were observed. Myers (1978) studied sexual dimorphism in 28 taxa of vespertilionid bats and found that the wing area was larger in females than in males of many species (16 species), even after making adjustments for body size differences. He concluded that phenomenon related to differences in aerodynamic demands between the sexes, with the larger area of female wings a requirement for coping with the increased load associated with carrying a fetus. The same principle may explain the compensation in asymmetry found in the structures composing the wings of *D. rotundus*. The females reveal less total variation in wing area than males; moreover, no asymmetry in wing area was revealed. This leads to the conclusion that for females, selection is acting mainly in relation to the maintenance of wing size and shape, since compensation to maintain them should diminish eventual aerodynamic problems.

The cost of the maintenance of symmetry is high. There is thus a trade-off between the development/maintenance of symmetry and functional aspects, with small degrees of asymmetry maintained in the population. It is possible that the relationship between functionality and asymmetric development results in structures with greater adaptive value, and that these will eventually develop into a more functional structure with a stable form (Møller and Swaddle 1997).

The maintenance of the symmetry of overall wing area in the females suggests that the selection involved promotes the process of flight, especially if they have to take its pup together, since the individual structures vary greatly. However, the observed phenomenon concerning asymmetry (and its compensation) was restricted to a single colony. Thus, it may be treated for the moment as an isolated case, not as a "tendency" or a morphosis.

In conclusion, there are significant differences in the sizes/lengths of the structures comprising the wings of the studied *D. rotundus* population. However, their effects on the area of the wings are generally minimized by compensations due to differential growth on the opposite size. Although evolution acts to maintain symmetry, this is the symmetry of the whole, not of the parts, because what is important for flight is the symmetry related to the wing function. However, to verify if this pattern occurs in other populations or other species, further research is strongly recommended. Particularly important will be studies focusing in other bat species (with different diets, behaviors, aggregation patterns) living under different levels of environmental stress.

Those studies will certainly allow the effective comprehension regarding the effects of the habitat determining different types of asymmetry, and also permit the evaluation of how the environmental stress level can determine different kinds of asymmetry.

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